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Microalgal populations of three New Zealand coastal locations: forcing functions and benthic-pelagic links

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ABSTRACT: I investigated spatial and temporal variability in benthic and pelagic (phytoplankton) microalgal assemblages in 2 harbours and a coastal embayment off the east coast of the North Island of New Zealand in late spring, summer and autumn. For the first time pelagic microalgal assemblages were sampled just above the sediment in the layer from which suspension feeders are likely to feed (~10 cm). Benthic microalgal assemblages were also assessed within the sediments. Strong links were observed between pelagic and benthic microalgal populations, with the amount of benthic microalgae found in suspension correlated with current speed and turbidity. Conversely, a number of species found within the benthic counts were tychopelagic species whose life habit is to rely on currents which re-suspend them from the benthic to pelagic environment. In late spring, pelagic water samples from 1 harbour and the embayment it opened into were dominated by dinoflagellate taxa, while diatoms dominated the second harbour location. In autumn, all the locations were dominated by diatom taxa but the 2 harbours were most similar in community composition. In summer, local conditions favoured the development of different microalgal populations in each location. Both pelagic and benthic microalgal assemblages generally decreased in similarity as spatial scale increased, with populations being most similar within a sampling site and least similar between locations. Benthic microalgae assemblages were more variable than pelagic assemblages within and between sampling sites at the locations, but had a greater similarity between locations (40 to 64%). Our results provide a new insight into the scales of variability of microalgal populations within and between different nearshore environments, and identify some of the forcing factors that drive changes in microalgal composition. By sampling microalgal populations just above the sediment we have begun to characterise the microalgal communities that sustain suspension feeders.

KEY WORDS: Pelagic · Benthic · Microalgae · Resuspension · Turbidity · Variability

INTRODUCTION

Microalgae are key biota in nearshore coastal waters, affecting food web structure, water quality, and trophic transfer efficiencies (Jumars et al. 1993, Lalli & Parsons 1997). In particular, they form part of a strong link between the water column and the seafloor. Pelagic phytoplankton and re-suspended benthic algae are a primary food supply for benthic macrofaunal suspension feeders (Hickman et. al. 1991, de Jonge & van Beusekom 1992, Muschenheim & Newell 1992, Herman et al. 2000). These animals are often able to preferentially select particles for ingestion (Shumway et al. 1985, Ward et al. 1998, Dupuy et al. 1999), such that size, morphology and nutritional content of the algae are frequently more important than overall biomass. Settling pelagic phytoplankton and benthic algae are a food source for macrofaunal deposit feeders (de Jonge & van Beusekom 1992, Muschenheim & Newell 1992, Herman et al. 2000). Benthic algae, of certain morphologies and/or densities, can also increase the cohesiveness of sediments, thus reducing resuspension of sediments (Delgado et al. 1991, Stal 1994). Despite the importance of microalgae,

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we do not fully understand what drives microalgal community composition, or the differences observed between and within locations.

Generally, in euhaline environments open to tidal flushing and the influence of offshore waters, large-scale phytoplankton dynamics are controlled by water circulation and temperature-driven patterns (Mallin 1994). In many turbid estuaries, light is believed to be the limiting factor for phytoplankton growth (Cloern 1987); however, increased turbidity may be associated with increases in phytoplankton biomass (Snow et al. 2000). Exposure to waves and strong currents can also affect algal composition. Often the 'phytoplankton' of shallow nearshore environments are found to contain a large proportion of re-suspended benthic microalgae (Baillie & Welsh 1980, Shaffer & Sullivan 1988, de Jonge & van Beusekom 1992, Muschenheim & Newell 1992). The amount of resuspension that occurs is dependent on both the physical factors affecting sediment resuspension (waves and currents) and the size, morphology and behavioural characteristics of the algae present in the benthos (Stal 1994). Some re-suspended microalgae in such systems are 'tycho-pelagic' (Cahoon & Laws 1993). Tychopelagic species rely on currents to re-suspend them from the benthic to pelagic environment. They alternatively sink to the bottom of the system and are re-suspended by physical processes. Thus, the linkage between the pelagic and the benthic environment is complex, having a major influence on the microalgal composition and production in shallow water systems. In turn, changes in these microalgal assemblages directly affect benthic suspension feeders (Hickman et al. 1991, Herman et al. 2000).

This study investigates the structure of microalgal assemblages found in 3 shallow-water coastal systems in New Zealand and concentrates on the link between the benthic and pelagic microalgal assemblages by sampling both the benthos and the water ~10 cm above the sediment. I identified the variability associated with large-scale factors (seasonal and circulation) by sampling over the late spring to autumn in 2 well-separated harbours and a coastal embayment adjacent to 1 of the harbours (scales of km to 100s of km). Smaller-scale variability was also examined by sampling at 2 hierarchical levels (10s of m, and 100s of m to km) within each system. This sampling design allowed me to make a number of predictions about the structure and functioning of microalgal communities. I predicted that: (1) the amount of benthic microalgae found in the overlying pelagic water would be related to wave and/or current conditions and the size and morphology of benthic algae; (2) the community composition would be related to turbidity; (3) pelagic and benthic microalgal population variability would be influenced more by seasonal variation than local physical conditions; (4) the similarity between locations in pelagic microalgal communities would be driven by physical forcing functions and/or water circulation (i.e. either the 2 harbours or the harbour and adjacent coastal embayment would be more similar); (5) the benthic microalgae assemblages would be more affected by small-scale habitat differences than pelagic microalgae, i.e. I would find more variation between benthic microalgae populations at the small scale (10s of m) than at the large (km to 100s of km), or medium (100s of m to km) scales.

Currently, little is known about the level of interaction between benthic and pelagic microalgal populations near the sediment surface, and how hydrodynamics affect these interactions. By sampling these microalgal populations I also hope to gain a better understanding of the microalgal communities grazed by suspension feeders. Furthermore, little is known about the scales at which microalgal populations vary. By addressing these issues, and investigating these predictions for the first time in New Zealand waters, I hope to extend our understanding of near-shore microalgal communities.

MATERIALS AND METHODS

Sampling sites. Three coastal locations were investigated at North Island, New Zealand (Fig. 1). Mahurangi Harbour (25 km^2) is a drowned river valley with small areas of intertidal flats. The subtidal drainage channel is well mixed with relatively strong tidal flows (max ~50 cm s^{-1} at 100 cm above bed). Tauranga Harbour (200 km^2) is a barrier island estuary, much larger than Mahurangi, with extensive intertidal flats dissected by subtidal drainage channels. The third location, Kawau Bay, is a sheltered embayment adjacent to Mahurangi Harbour.

The 3 selected locations (Fig. 1) represent different hydrodynamic conditions, and were expected to have different background levels of suspended sediment and turbidity. All locations had semi-diurnal tides of between 3 and 4 m.

Within each location, 3 sites were sampled (Fig. 1). The sampling sites had similar sediment grain sizes, water depths and tidal flows and were separated by no more than 10 min boat time, to ensure that sampling at all sites could be carried out within 30 min. All sampling locations were in subtidal areas with mean water depths between 2.5 and 8.5 m. The 3 sites chosen within each location represented 3 different mean water depths: at each location there was a ~3 , ~5 and ~8 m deep site. The same depths were selected at each location to identify any water depth effects when comparing sites. Time series samples were collected for

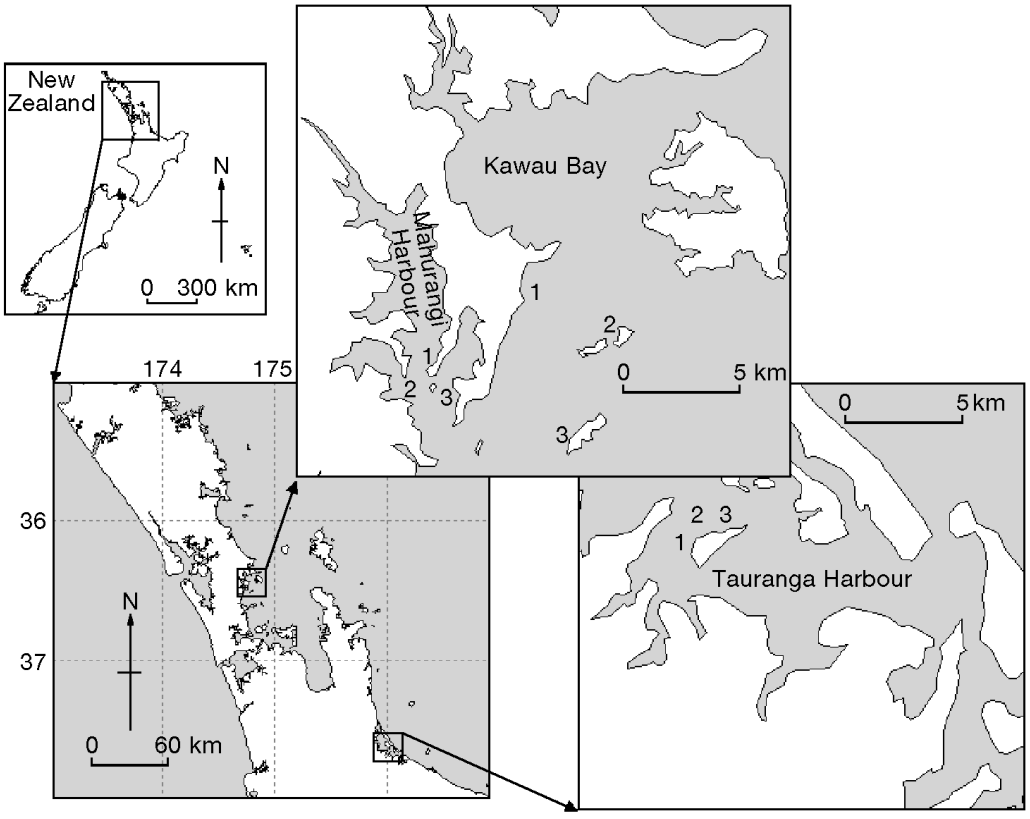

Fig. 1. North Island of New Zealand, with coastal sampling sites (1 to 3) in Kawau Bay, Mahurangi Harbour, and Tauranga Harbour

each site in November 1999 (late spring), January 2000 (summer) and April 2000 (autumn). Water temperatures showed little variation between sites, ranging from 17 to 19°C in November, 23 to 25°C in January and 18 to 19°C in April. Samples were always taken between spring-neap phases of the tidal cycle. On average our sampling days were 4.3 d out of phase with neap tidal cycles and 5.9 d out of phase with spring tidal cycles, allowing our estimates of biomass to be a more average representation of monthly biomass levels.

Within-site spatial and temporal sampling. Two sites per hour were sampled over a 12 h period to encompass the full range of the semi-diurnal tidal cycle. At each site, 3 replicate water samples were taken approximately 10 cm above the sediment surface, at 10 m intervals along a marked transect using a diver-operated, horizontal Van Dorn bottle. Subsamples (~100 ml) of each water sample were placed on ice in the dark for later analysis of turbidity. Other subsamples for phytoplankton analysis were preserved in 1% Lugol's iodine and bulked over the 12 h time period. At midday, sediment samples were taken using a 2 cm diameter corer. Samples for algal composition were taken to a depth of 2 cm in the muddy sediments and to 4 cm in the sandy sediments. Samples for algal composition were immediately preserved in Lugol's iodine solution (final conc. 10%).

Hydrodynamic variables. Electromagnetic current meters (S4, Interocean) were used to measure currents 0.5 m above the bed, by sampling for 5 min, every 10 min. We measured each site over 15 d, from neap to spring tide. As we only had 3 S4s, currents at each location were measured on separate occasions over March/April. Current speeds 10 cm above the bed were calculated by a standard log velocity profile with an assumed flat bed roughness. A maximum, mean and minimum current speed was then calculated for each site. DOBIE wave gauges (NIWA Instrument Systems) were used to measure waves occurring at each site over a 15 d period, at the same time as the currents were measured. DOBIEs measure pressure fluctuations and calculate a series of wave statistics, including significant wave height and wave energy dissipated on the bed by friction. Measurements were collected in bursts at 30 min intervals, with each burst consisting of 2048 data points at an interval of 0.2 s. For each site, the mean significant wave height and total amount of wave energy dissipated over the 15 d period were calculated.

Sample analysis. In the laboratory, water and sediment samples were examined for microalgal content, in Utermöhl chambers on a Leitz inverted microscope.

For the water samples, 100 ml was settled for 24 h. Sediment cores were initially re-suspended in approximately 10 ml of water and then a 5 ml subsample of the re-suspended material was analysed. Microalgae were identified to species level where possible (Fenchel 1982, Sournia 1986, Chretiennot-Dinet et al. 1990, Patterson & Larson 1991, Throndsen 1993, Tomas 1997). Multiple species within a genera that could not be identified to species level were categorised by morphology, i.e. *Skeletonema* sp. #1 and *Skeletonema* sp. #2. Pelagic microalgae were fully enumerated. Benthic microalgae numbers were counted within the 5 ml subsample of the re-suspended material. Benthic species were then ranked by total biovolume within the subsample on a scale of 1 to 10, with 1 being the most dominant species 10 being the least dominant. Biomass for all algal populations was calculated using cell numbers and taxa biovolumes estimated using formulae representing the geometrical solids that approximated cell shape (Rott 1981, Hillebrand et al. 1999). Within ~2 h of collection, the chilled unpreserved water samples were read for turbidity on a HACH 2100AN Turbidimeter.

Analysis of the microalgal population assemblages. Microalgae were categorised and grouped in a number of ways for analysis of temporal and spatial patterns. The first resolution used was that of species, followed by families. Families were then grouped together into 5 divisions based on the dominant phytoplankton divisions found at the different coastal locations. These divisions were: thecate dinoflagellates, naked dinoflagellates, centric diatoms, pennate diatoms and a final grouping described as 'Others' that included silicoflagellates, cryptomonads, euglenoids and prymnesiophytes.

Functional size categories were calculated, with each species identified being classified into 1 of 4 size categories based on cell size. The size classes were >200 µm (mesophytoplankton), 20 to 200 µm (microphytoplankton), 5 to 20 µm (nanophytoplankton) and a small cell category <5 µm. The <5 µm category did not account for picophytoplankton 0.2 to 2 µm, nor could it fully estimate the biomass of other <5 µm cells, as some small cells are known to burst on preservation with Lugol's iodine (Jeffrey & Vesk 1997).

Morphological characteristics were also used to group species as a specific type: single cells, simple chain, zig-zag chain, and stepped chain. These categories were defined following Tomas (1997), as: 'single cells' describing cells always found alone (unattached), except in some cases for reproduction; 'simple chains' used to describe cells forming colonies in a simple straight chain such as *Skeletonema*, *Chaetoceros*; 'zig-zag chain' used to describe cells connected by mucilage pads such as *Thalassionema*, forming a zig-zag or star shaped pattern; 'stepped chain' to describe cells that overlap at their ends like *Pseudonitzschia.* This categorisation was described as 'morphotype' in further analysis.

Finally, for comparison between benthic and pelagic algal assemblages, taxa were placed into broad groups based on their predominant habitat. Taxa were categorised as benthic, pelagic or tychopelagic. The tychopelagic category was included to allow an estimation of species/genera whose life habit was to rely on currents to re-suspend then from the benthic to pelagic environment.

Statistical analyses. Variability in algal communities was assessed using Bray-Curtis similarities (SIMPER, Clarke 1993) on biovolume biomass grouped into various categories (species, families, divisions etc). Within-site and between-site variability was assessed on each date, for each area separately, using all replicates (SIMPER, Clarke 1993). Significance of differences between sites was tested using ANOSIM, a randomisation test (PRIMER, Clarke & Warwick 1994). Replicates were averaged over each site before within location and between location variability was assessed for each date, and differences between locations tested for significance. Finally, comparisons of between location and between date variability were made. All similarities were calculated from raw data, except when comparisons between benthic and pelagic data were being made, and then the pelagic data was rank transformed to approximate benthic data.

Relationships between resuspended algae found in the water column and hydrodynamic variables were assessed using multiple regression analysis with a binomial error structure. The percentage of resuspended algae found at each site was averaged over the 3 sampling dates before being used as the dependent variable. Non-linearity of response was investigated by using log and exponential transformations of the hydrodynamic variables. Backwards selection with an exit value of 0.15 was used to produce the most parsimonious model. The stability of the final model to the order in which variables were removed was checked.

Correlations between pelagic algal data and turbidity were investigated using Pearson's product-moment r (DATADESK 6.1, Velleman 1992) for selected data groups. All available data from all sampling dates were used in 1 analysis.

RESULTS

A summary of the major pelagic microalgal taxa (phytoplankton) and microalgal taxa observed in the benthos (tychopelagic and benthic) is presented in Appendix 1.

Effect of currents, waves and turbidity on microalgal populations

Pelagic counts revealed that on average between ~1 and 23% of the biomass ~10 cm above the sediment was benthic in origin. In areas of high mean current flow, tychopelagic species dominated the microalgal counts in the benthos. Multiple regression analysis showed that current speed accounted for 87% of the variation observed in the percentage of benthic microalgae found in suspension. Log average current speed worked to increase the percentage (χ^2 = 9.05, p = 0.0026, with a model deviation [dev]/total dev = 0.96, df = 7) while minimum current speeds worked to decrease the percentage (χ^2 = 9.19, p = 0.0024, with a model dev/total dev = 0.96, df = 7). No wave-related variables were important, possibly because this data was not available for the period before each sampling. The mean current speed statistics we used were calculated over 1 neap to spring tidal cycle and are therefore more likely to be representative of those occurring throughout the year. Maximum, minimum and average current speeds are listed in Table 1.

In addition to current speed, turbidity showed some strong relationships with microalgal populations. Turbidity was consistently highest at Mahurangi Harbour, followed by Tauranga Harbour, with Kawau Bay always reporting the lowest mean turbidity levels within any sampling period (Fig. 2). Turbidity was significantly, though weakly (r = 0.49, p < 0.001, n = 73), correlated to the percentage of microalgae from the benthos reported in suspension (pelagic counts). Turbidity was negatively correlated to the percentage of centric diatoms (these were generally large, >180 µm) reported in the phytoplankton throughout the study (r = –0.26, p < 0.05, n = 73) and positively correlated to the percentage of silicoflagellates, cryptomonads, and euglenoids ('Others' category) (r = 0.31, p < 0.01, n = 72), which were predominately small cells (<10 µm). In addition, in January and April, turbidity was highly positively correlated to the percentage of <5 µm biovolume (r = 0.53, r = 0.60; p < 0.001, n = 72, respectively), while always being negatively correlated to the percentage of large cells >180 µm in April (r = –0.37, p < 0.001, n = 73).

Table 1. Current speeds (cm s^{-1}) recorded over neap to spring tidal cycles at 3 locations in 3 sampling sites: Kawau Bay (KAW), Mahurangi Harbour (MAH) and Tauranga Harbour (TAU); ND = no data

	Mean	Maximum	Minimum
KAW1	3.49	7.06	0.31
KAW2	3.21	13.00	0.09
KAW3	ND	ND	ND
MAH1	9.03	22.60	0.94
MAH2	4.09	13.04	0.10
MAH3	5.39	12.08	0.04
TAU1	9.53	23.23	0.04
TAU2	11.03	29.23	0.20
TAU3	13.44	33.96	0.47

Phytoplankton population variability

Phytoplankton populations differed more on the scale of between seasons than between locations (Fig. 3), with an average similarity (across locations) of only 9%. The large seasonal changes in biomass were predominantly driven by the presence of different taxa. (Figs. 3 & 4A, Table 2).

Between locations, within a season, similarities were higher (Fig. 3, Table 2). In late spring, Kawau Bay and Mahurangi Harbour were the most similar (49%), with Tauranga Harbour clearly different (Tables 2 & 3, Fig. 3). These results reflected the changes observed in phytoplankton taxa (Fig. 4, Table 2). In summer, all locations differed by more than 80% (Table 3, Fig. 3), again reflecting the changes observed in phytoplankton taxa (Fig. 4, Table 2). In autumn, Tauranga and Mahurangi were the most similar (37%) (Table 3, Fig. 3). Phytoplankton biomass at all 3 sites was dominated by diatom taxa, but both dinoflagellates and other genera also made major contributions to the biomass in all 3 locations (Fig. 4, Table 2).

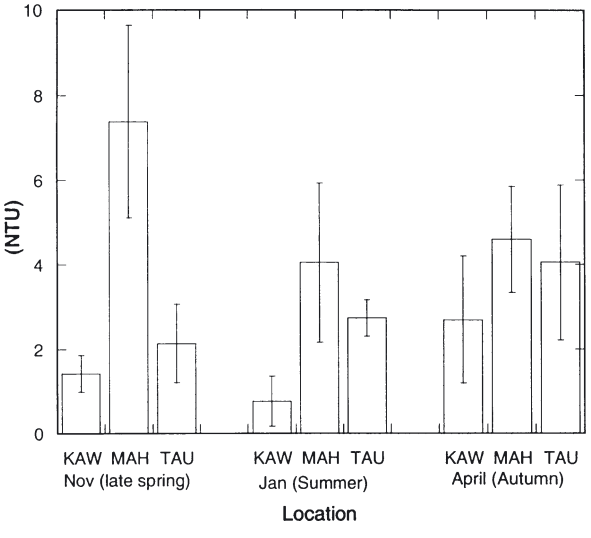

Fig. 2. Turbidity (nephelometer turbitity units; NTU). Sampling locations; Kawau Bay (KAW), Mahurangi Harbour (MAH), and Tauranga Harbour (TAU). Season; late spring (November), summer (January) and autumn (April). Error bars show 1 SD

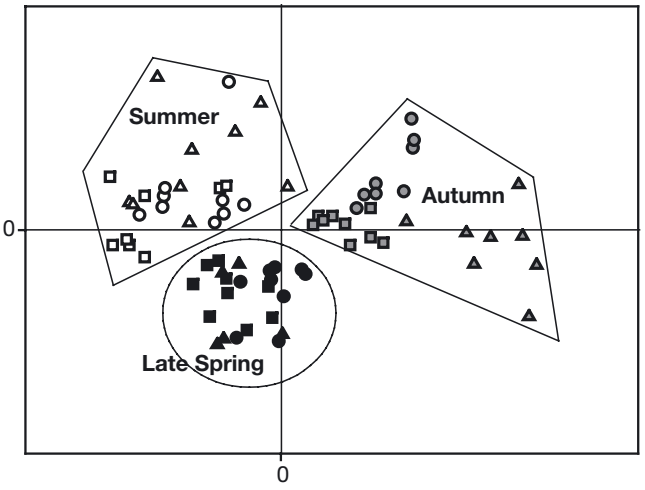

Fig. 3. Ordination plot of phytoplankton biomass based on 'family' biovolume at 78 sites transformed using a 2D similarity/distance matrix generated from Primer (minimum stress 0.19). ▲: Mahurangi Harbour (MAH) in spring, ■: Tauranga Harbour (TAU) in spring, ●: Kawau Bay (KAW) in spring, △: MAH in summer, □: TAU in summer, ○: KAW in summer, ▲: MAH in autumn, ●: KAW in autumn, ■: TAU in autumn. Seasonal regions were added manually

ANOSIM (based on 'Family' biovolume), conducted between and within sites (Table 4, Fig. 1), indicated that phytoplankton was most similar within sites and became less similar as the sampling scale increased. The only exception was Mahurangi Harbour in summer, where there was more variation within than between sites (Table 4). In contrast, in autumn Mahurangi Harbour showed the greatest similarity between sites of any location, while Tauranga Harbour in summer showed the least similarity between sites (Table 4).

Microalgae in the benthos

Microscope examination of microalgae within the benthos allowed the separation of genera into 3 different categories, based on the life habit of the microalgal populations observed: benthic microalgae, pelagic microalgae (sedimented) and tychopelagic. Microalgal composition within the benthos showed more similarity between seasons than was observed in the pelagic

Table 2. Dominant pelagic microalgal taxa at the sampling locations

	Naked dinoflagellates	Thecate dinoflagellates	Centric diatoms	Pennate diatoms
Late spring				
Kawau Bay	*Gyrodinium* spp. *Gymnodinium* spp.	*Ceratium furca* *C. fusus* *Protoperidinium* sp.	*Rhizosolenia* spp. *Skeletonema* sp.	*Nitzschia* spp.
Mahurangi Harbour	Gyrodinium spp. Gymnodinium spp.	*Ceratium furca* *C. fusus* *Protoperidinim* sp.	*Rhizosolenia* spp. *Leptocylindricus* spp.	*Pleurosigma* sp. *Navicula* sp.
Tauranga Harbour	*Gymnodinium* spp.	*Protoperidinim* sp.	*Chaetoceros* spp.	*Pseudonitzschia* sp. *Nitzschia* spp.
Summer				
Kawau Bay	*Noctiluca scintillans*	*Ceratium furca* *C. fusus*	*Rhizosolenia* spp. *Leptocylindricus danicus*	*Thalassiothrix* sp.
Mahurangi Harbour	*Gyrodinium* sp. *Gymnodinium* spp.	*Ceratium furca* *C. fusus*	*Chaetoceros* spp.	*Thalassiothrix* sp.
Tauranga Harbour	*Gymnodinium* sp.	*Scrippsiella trochoidea* *Protoperidinium* sp.	*Chaetoceros* spp. *Gyrosigma* sp. *Pseudonitzschia* sp. *Nitzschia* spp.	*Thalassiosira* sp.
Autumn				
Kawau Bay	*Noctiluca scintillans*	*Scrippsiella trochoidea* *Protoperidinium* sp. *Prorocentrum* sp.	*Rhizosolenia* spp. *Leptocylindricus danicus* *Chaetoceros* spp.	*Gyrosigma* sp. *Nitzschia* spp. *Pleurosigma* sp. *Navicula* sp.
Mahurangi Harbour	*Gymnodinium* spp.	*Scrippsiella trochoidea* *Protoperidinium* sp.	*Eucampia* sp. *Rhizosolenia* sp. *Chaetoceros* sp.	*Diploneis* sp. *Navicula* sp. *Nitzschia* spp.
Tauranga Harbour	*Gymnodinium* sp. *Protoperidinium* sp.	*Scrippsiella trochoidea* *Eucampia* sp.	*Chaetoceros* sp. *Nitzschia* spp. *Rhizosolenia* sp.	*Navicula* sp.

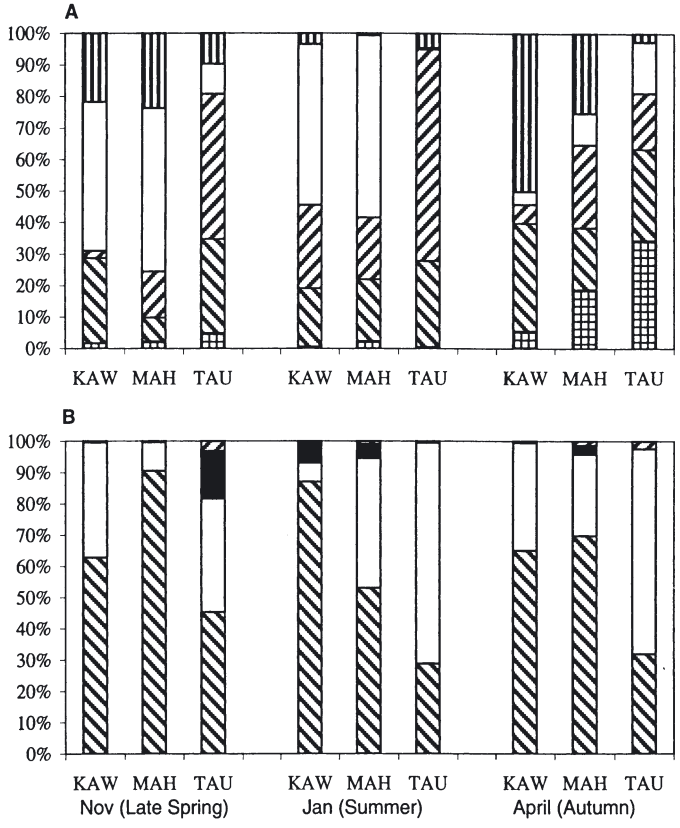

Fig. 4. (A) Phytoplankton biovolume (μm^3) grouped by 'division' as % of total biovolume biomass at the 3 coastal locations: Kawau Bay (KAW), Mahurangi Harbour (MAH), and Tauranga Harbour (TAU). ▨: diatoms (centric); ▨: diatoms (pennate); □: dinoflagellates (thecate); ▥: dinoflagellates (naked); ⊞: others (Silicoflagellates, Cryptomonads, Euglenoids). (B) Phytoplankton biovolume (μm^3) grouped by 'morphotype' as a percentage of total biovolume biomass at the 3 coastal locations; ▨: single cells; □: simple chain; ▨: zig-zag chain; ■: stepped chain

phytoplankton counts (Fig. 5). On average there was a 46% similarity between locations, between seasons. When all 3 populations within the benthos were examined at the scale of 'between locations' we observed some interesting differences within the seasons.

Table 3. Average percentage (%) similarity of pelagic and benthic microalgal populations between locations for the 3 sampling seasons. All results from analysing the biomass biovolume by 'family'. KAW = Kawau Bay, MAH = Mahurangi Harbour, TAU = Tauranga Harbour

	KAW & TAU	KAW & MAH	MAH & TAU
Late spring pelagic	49	18	29
Summer pelagic	19	11	2
Autumn pelagic	23	21	37
Late spring benthic	45	41	40
Summer benthic	47	53	46
Autumn benthic	64	45	44

In late spring, all 3 sites were similar, with calculated similarities between 40 and 45% (Table 3). The benthic microalgae taxa *Nitzschia* and *Navicula* dominated the counts at Kawau Bay and Tauranga Harbour. Tychopelagic cells were also important at these 2 locations, with *Gyrosigma* and *Pleurosigma* taxa being the major contributors to biomass. In Mahurangi Harbour, tychopelagic cells instead of benthic microalgal species dominated the benthic biomass with *Gyrosigma* and *Pleurosigma* taxa being the most abundant, while benthic *Nitzschia* and *Navicula* taxa were less important. The most abundant pelagic species observed in the benthic samples varied with location, with *Bacillaria paxillifer* being dominant at Mahurangi Harbour, *Pseudonitzschia* sp. at Kawau Bay and *Thalassiosira nitzschioides* in Tauranga Harbour.

In summer, the similarity of microalgae within the benthos increased between locations. Kawau Bay and Mahurangi Harbour were the most similar (53%) (Table 3), reflecting similarities in the dominant benthic taxa (*Amphora*, *Nitzschia* and *Navicula* sp.) and pelagic taxon (*Nitzschia closterium*). In Tauranga Harbour, tychopelagic cells dominated (*Gyrosigma*, *Pleurosigma* and *Paralia* sp.)

In autumn, a different pattern was observed; Tauranga Harbour and Kawau Bay were most similar (64%) (Table 3), and dominated by tychopelagic cells

Table 4. Average percentage (%) similarity for pelagic and benthic microalgal populations analysing the biomass biovolume by 'family' within and between sites during our 3 sampling periods. KAW = Kawau Bay, MAH = Mahurangi Harbour, TAU = Tauranga Harbour

	KAW Within sites	KAW Between sites	MAH Within sites	MAH Between sites	TAU Within sites	TAU Between sites
Late spring pelagic	75	66	65	40	79	71
Summer pelagic	71	55	60	60	55	37
Autumn pelagic	65	63	85	84	61	44
Late spring benthic	65	61	87	58	66	63
Summer benthic	81	59	62	48	79	60
Autumn benthic	77	75	59	58	71	69

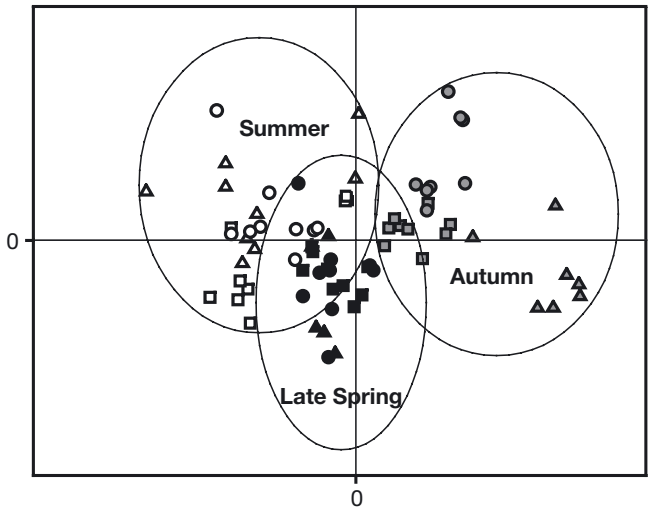

Fig. 5. Ordination plot of benthic microalgal biomass based on biovolume at 78 sites transformed using a 2D similarity/ distance matrix generated from Primer (minimum stress 0.15). ▲: Mahurangi Harbour (MAH) in spring, ■: Tauranga Harbour (TAU) in spring, ●: Kawau Bay (KAW) in spring, △: MAH in summer, □: TAU in summer, ○: KAW in summer, ▲: MAH in autumn, ■: KAW in autumn, ●: TAU in autumn. Seasonal regions were added manually

(*Gyrosigma* and *Pleurosigma* sp.), although benthic cyanobacterial filaments (*Oscillatoria* spp.) were observed in high numbers at all 3 locations. The most abundant pelagic taxa observed in the sediment at Kawau Bay and Mahurangi Harbour was *Bacillaria paxllifar*, whereas in Tauranga Harbour *Thalassiosira nitzschioides* was important. Biomass estimates calculated by multiplying the reported cell numbers by mean cell biovolumes indicated that biomass increased in summer and remained high at all locations in autumn.

ANOSIM of microalgae found in the sediment (based on 'family' biovolume) was also conducted at the scales of between and within sites (Table 4, Fig 1). Benthic microalgal populations were generally more similar at these smaller scales, with similarities increasing as the sample scales became smaller (Table 4).

Table 5. Average percentage (%) similarity for benthic and pelagic microalgal populations at 3 measurement scales analysing the biomass biovolume by 'family'

	Within sites at a location	Between sites within a location	Between locations
Benthic algae	72	61	47
Pelagic algae	74	69	34

Comparative scales of variability in benthic and pelagic microalgal populations

In order to compare the benthic microalgal counts from the benthos with pelagic data, raw pelagic data were transformed to approximate rank abundance. This process increased the similarities reported for pelagic microalgae, but did not affect the observed trends in data. The results showed benthic microalgal biomass had the greatest similarity between locations (47%), whereas pelagic microalgae were more similar between sites within a location (69%) and within sites at a location (74%) (Table 5).

DISCUSSION

Currents, waves and turbidly effects on microalgal communities

In the water column, as predicted, the biomass of both resuspended tychopelagic and benthic microalgae increased with mean current speed. Other studies have reported large amounts of resuspended benthic algae in the 'phytoplankton' of shallow nearshore environments (Baillie & Welsh 1980, Shaffer & Sullivan 1988, de Jonge & van Beusekom 1992, Muschenheim & Newell 1992). The proportion of benthic algae as biomass was similar to that reported by Lucas et al. (2001) but lower than that calculated by de Jonge & van Beusekom (1995). Tychopelagic taxa dominated both water column and benthic sediment samples, where high mean current speeds were reported probably because this allows them to remain in the water column longer, giving them maximum exposure to higher mean light levels for growth. Simultaneously, higher current flows increase turbidity by resuspending both algae and sediment, and decreasing the light levels available to benthic microalgae. In contrast, benthic species, which were generally bound onto the sediment surface, colonial, or were fast to sink, dominated the benthos in locations with low mean current speeds. These results suggest that, as reported in many turbid estuaries (Cloern 1987), light is likely to be an important limiting factor for phytoplankton and benthic algal growth at our locations.

Increased current speeds led to increased turbidity and lower benthic biomasses in the benthos, as has been reported elsewhere (Lucas et al. 2001). The relative amount of tychopelagic microalgae found in the benthos increased in late spring and autumn when turbidity increased, but this pattern was not always observed in summer. In summer, Mahurangi Harbour benthic microalgae biomass exceeded tychopelagic microalgae in the benthos, despite high turbidity being reported at this location. This result may be due to the

high summer light levels penetrating to the benthos, and allowing benthic microalgae a favourable environment to establish populations in sediment at this time. It is important to recognise that other factors beyond the scope of this study, such as grazing, will also have impacted on these populations. Muschenheim & Newell (1992) found that mussels fed preferentially on high concentrations of resuspended benthic diatoms, and other studies suggest increased turbulence leads to more grazing by microzooplankton and perhaps zooplankton species by increasing predator-prey encounter rates (Peters et al. 2002).

The phytoplankton community composition was related to turbidity. Turbidity was negatively correlated to the largest size class, >180 µm, and positively correlated to <5 µm biovolume biomass and Silicoflagellates, Cryptomonads, and Euglenoids. This suggested that bigger phytoplankton cells (that were not tychopelagic) were less able to cope with sediment loading and were not well adapted to turbid low light conditions. These results correspond to reports that larger phytoplankton cells can be rapidly removed from the water column when exposed to increasing sediment loads (Burkholder 1992).

Seasonal variation in phytoplankton populations

The changes in phytoplankton biomass and composition followed seasonal changes observed in New Zealand and overseas (Cloern 1987, Bradford-Grieve et al. 1997). In late spring, phytoplankton biomass was low and dominated by dinoflagellates.

In summer, phytoplankton biomass increased at 2 locations and diatoms dominated the biomass at all 3 locations, consistent with reports from estuarine environments (Mallin 1994, Vant & Safi 1996), but different to reports on coastal phytoplankton populations (see Chang et al. 2003). In estuarine environments, increasing light and temperature levels and/or the release of regenerated nutrients in summer has been reported to result in increased production and increased summer biomass (Taft et al. 1980, Boyton et al. 1982, Malone et al. 1986, Mallin 1994, Vant & Safi 1996, Lucas et al. 2001). In autumn, the phytoplankton biomass declined at the 2 locations that reported an increase in summer. Small diatoms dominated and small flagellates and naked dinoflagellates, rather than thecate dinoflagellates, increased in importance. Other studies have suggested that, in autumn, declining light levels and water temperatures begin to limit phytoplankton growth while grazing pressure remains high (Gibbs & Vant 1997, Ross et al. 1998). Associated with this decline in biomass, smaller flagellated cells generally become more dominant (Malone 1980).

Some studies have shown that phytoplankton populations can also vary considerably in the short-term due to the effects of spring-neap tidal cycles (Lauria et al. 1999). In this study I minimised these effects by sampling at intervals between neap and spring tidal cycles, providing a more average representation of seasonal biomass. While some taxa may be favoured by different phases of the tidal cycle, this effect would be minimised at the sampling depth (10 cm above the sediment) where cells that can actively maintain their buoyancy are less likely to occur.

Relative importance of circulation patterns versus physical forcing factors on phytoplankton

Seasonal changes may have dominated phytoplankton composition, but spatial changes were important in modifying seasonal effects. I predicted that the similarity between locations in pelagic microalgal communities would be driven by physical forcing functions and/or water circulation. In late spring, I found the physically linked locations of Kawau Bay and Mahurangi Harbour were similar in biomass and species composition. This indicated that the pelagic microalgal communities at this time were driven more by large-scale circulation than by local physical forcing functions. Conversely, in autumn the Mahurangi and Tauranga locations, which were both harbours, were more similar in biomass and species composition. At this time physical forcing factors, such as currents, wave action and turbidity, appear to have had the most influence on the phytoplankton composition. In summer, the least similarity was observed between locations, suggesting local physical forcing factors favoured the development of different phytoplankton populations at this time. Overall, these results indicated that both circulation and physical forcing factors are important.

Some interesting spatial-temporal patterns were observed. Mahurangi Harbour phytoplankton biomass peaked in autumn, whereas the other coastal locations peaked in summer. Mahurangi Harbour in summer also had a similar biomass and species composition to Kawau Bay in late spring (November), suggesting a similar phytoplankton succession but with a time lag. Although Mahurangi Harbour and Kawau Bay were less similar in summer and autumn, they were still both dominated by non chain-forming morphotypes, whereas Tauranga Harbour was dominated by chain-forming morphotypes. This result again suggests that circulation patterns are important at all times in determining phytoplankton populations, with local forcing factors modifying this effect to different degrees at different locations.

Overall, the results suggest that seasonal changes have the greatest influence on phytoplankton populations, but the timing and degree of these changes is modified by local forcing factors and circulation patterns, which combine to affect the composition and biomass of phytoplankton. At locations where light becomes limited due to turbidity (currents and runoff), it limits production and modifies seasonal patterns. This in turn has important implications for estuarine health, and indicates that currents, sediment loading and runoff will affect the food quantity and quality available for grazers.

Temporal and spatial variation in benthic microalgal populations

In contrast to my predictions, spatial changes in benthic microalgal populations between locations were as strong as seasonal changes, with both having, on average, a similarity of 46%. This result indicated that seasonal changes in light and temperature were only as influential on benthic microalgal taxa composition as local conditions.

The benthic and tychopelagic species observed were broadly similar to those species reported in other nearshore New Zealand locations and elsewhere (Gillespie et al. 2000, Lucas et al. 2001). Although diatoms dominated throughout the sampling period, cyanobacterial taxa (*Oscillatoria*) were also reported as important in autumn. These cyanobacterial microalgae appear to have been increased in number from late spring, and their ability to bind sand grains and reduce the erodibility of sandy sediments (Stal 1994) may have lead to the enhancement of benthic microalgal populations throughout the spring to autumn period.

Scales of variability in benthic versus pelagic microalgal populations

Benthic microalgae are generally recognised as being less mobile and more affected by small-scale habitat differences than pelagic microalgae (Mallin 1994, Lucas et al. 2001). The results confirmed this with similarity increasing as the spatial scales were reduced. However, benthic algal samples were more variable than pelagic populations at the smaller sampling scales of 10s of m and km (within sites and between sites), and more similar between locations (10s to 100s of km) (Tables 4 & 5). Pelagic microalgal similarities followed a similar pattern to the microalgae in the benthos, showing the greatest similarity at the smallest scale of within sites at a location (74%, Table 5), and decreasing in similarity to between locations (34%, Table 5). Pelagic microalgal similarities, however, continued to decrease as scales increased, with lower similarities being reported for pelagic microalgal between locations, and between locations between seasons. These results suggest that at this broad scale, physical factors may limit benthic diversity, whereas pelagic species vary more due to localised influences such as seed populations, tidal flushing, intrusions of offshore water, and the influence of runoff.

CONCLUSIONS

This study investigated microalgal abundance and variability, at a range of scales, in the benthos and in the water directly above the sediment bed where benthic suspension feeders feed. I explored the importance of physical factors such as circulation patterns, turbidity, and currents, and found that these factors were clearly important. Pelagic phytoplankton, tychopelagic microalgae and benthic microalgae were all found in the water column, all thus have the potential to be important food supplies for benthic macrofaunal suspension feeders.

Strong links between pelagic and benthic microalgal populations were identified, with resuspension by currents likely to be a key mechanism linking these populations. Although temporal/seasonal differences in microalgal assemblages are often recognised as important, circulation patterns were also important, with local physical-forcing factors modifying this effect to different degrees at different times. This study highlights the importance of spatial variations in understanding productivity, and suggests that such variations are likely to have important implications for macrofaunal suspension feeders.

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Appendix 1. Microalgal taxa observed during the study period. Genera are also classed into grouping based on life habit; P = pelagic, B = benthic, R = resuspendor

DINOFLAGELLATES	
Amphidinium sp.	P
Cachonina sp.	P
Ceratium furca (Ehr) Claparède et Lachmann	P
Ceratium fusus (Ehr) Dujardin	P
Ceratium tripos (O. F. Müller) Nitzch	P
Ceratium sp.	P
Dinophysis acuminata Claparède et Lachmann	P
Dinophysis spp.	P
Diplopsalis sp.	P
Gonyaulax sp.	P
Gymnodinium sanguineum Hirasaka	P
Gymnodinium spp.	PB
Gyrodinium spp.	P
Heterocapsa triquetra (Ehr) Balech	P
Heterocapsa sp.	P
Noctiluca scintillans (Macartney) Kofoid & Swezy	P
Peridinium sp.	P
Prorocentrum spp.	P
Protoperidinium brevipes (Paulsen) Balech	P
Protoperidinium spp.	P
Pyrocystis lunula (Schott) Schott	P
Scrippsiella trochoidea (Stein) Balech	P
Round dinoflagellate cyst	B
Unknown dinoflagellate	B
DIATOMS	
Amphora spp.	B
Asteromphalus sp.	P
Actinoptychus undulates Ehrenberg	P
Bacillaria paxillifera O. F. Moller	R
Biddulphia sp.	P
c.f. *Membraneis* sp.	B
c.f. *Trigonium* sp.	B
Raphoneis sp.	B
Campylodiscus innominatus	P
Cerataulina sp.	P
Chaetoceros convolutus Wm Smith	P
Chaetoceros brevis Schott	P
Chaetoceros decipiens Cleve	P
Chaetoceros spp.	P
Cocconeis sp.	B
Coscinodiscus spp.	R
Detonula spp.	R
Diploneis sp.	R
Dirylum brightwelli (T. West) Grunow	P
Entromoneis sp.	P
Eucampia cornuta	P
Eucampia zoodiacus Ehrenberg	P
Eucampia sp.	P
Fragilariopsis sp.	R
Grammatophora sp.	P
Guinardiaflaccida (Castracane) H. Peragallo	P
Guinnardia spp.	P
DIATOMS (continued)	
Gyrosigma sp.	R
Hemiaulus sp.	P
Lauderia annulata Cleve	P
Leptocylindricus danicus Cleve	P
Leptocylindricus minimus	P
Licmophora sp.	B
Lithodesmium spp.	R
Melosira sp.	P
Minidiscus sp.	R
Navicula spp.	BPR
Navicula ventricosa	B
Neodelphineis sp.	B
Pseudonitzschia spp.	P
Nitzschia closterium Ehrenberg (W. Smith)	R
Nitzschia longissima (Kutzing) Pritchard	R
Nitzchia seriata Cleve	B
Nitzschia sigmoidea	R
Nitzschia spp.	BPR
Paralia spp.	R
Pleurosigma sp.	R
Rhizosolenia robusta Pritchard	P
Rhizosolenia styliformis Brightwell	P
Rhizosolenia imbricata Brightwell	P
Rhizosolenia sp.	P
Skeletonema spp.	P
Stauropsis sp.	P
Stephanopyxis sp.	P
Surirella spp.	B
Thalassiosira hyalina	P
Thalassiosira spp.	R
Thalassionema nitzschioides (Grunow) Mereschkowsky	P
Thalassionema spp.	P
Thalassiothrix sp.	P
PRYMNESIOPHYTES	
Chrysochromulina sp.	P
OTHER (Silicoflagellates, Cryptomonads, Euglenoids)	
Cryptomonads	P
Dictyocha fibula Ehrenberg	R
Dictyocha speculum Ehrenberg	R
Dictyocha sp.	R
Eugleniod sp.	R
Oscillatoria spp.	B
Quadriflagellates	P
Small flagellates	PB
Green filament	B
CILIATES	
Unknown ciliates	BPR
Mesodinium rubrum Lohmann	P

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